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Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea

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ABSTRACT: Hydrography and larval fish distribution in the northeastern North Sea were studied during a research programme carried out during the period from 1991 to 1994. The aim was to examine the connection between frontal zone formation and nursery characteristics of gadoid larvae at the shelf break. Emphasis was placed on the year-to-year variation in frontal characteristics and distributional patterns of larvae. An area of about 67 000 km² covering the northeastern North Sea, the Skagerrak and the Kattegat was surveyed by grid or transect sampling. At each sampling station the hydrography was studied by CTD casts, and the abundance of fish larvae was measured by depth integrating tows of a 2 m ring net. Five species of gadoid larvae and small juveniles were found in the area: cod *Gadus morhua*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus*, Norway pout *Trisopterus esmarki* and saithe *Pollachius virens*. Larval abundance differed markedly between species and years. The abundance of all species was the highest in 1992 and declined during the following 2 years. In 1994, cod and whiting were the only gadoid species observed. Peak abundance of all gadoids was found in the vicinity of the frontal zone; however, the relationship between larval distribution and hydrography differed among species. Correspondence between spatial and interannual variation in characteristics of frontal zones and larval distributions suggests that frontal zone variability is a central element in the early life of gadoid larvae from the area.

KEY WORDS: Gadoid larvae · Distributional characteristics · Interannual variability · Hydrographic fronts · Plankton assemblages

INTRODUCTION

The early planktonic stages of marine fish depend strongly on physical oceanographic regimes and their variation. Diverging currents and turbulence disperse the initial high concentrations of newly spawned eggs and the degree of patchiness generally declines during the very early stages (McGurk 1987, Frank et al. 1993). Likewise, prevalent currents in the spawning area often advect the eggs and larvae over long distances (Hermann et al. 1996, Stabenø et al. 1996). On the other hand, the dispersion and advection during the early stages might be restricted or counteracted by a

number of other mechanisms. Okubo (1984) proposed that plankton aggregate because of: (1) behavioural reactions of the plankton to distributions of environmental factors, (2) food-chain association in predator-prey reactions, (3) aggregative behaviours for feeding, and (4) mechanical retention in convective cells or hydrographic fronts. Most likely an aggregation is the result of a variety of these or other processes acting in concert.

Processes related to the hydrographic fronts (the boundary zones between dissimilar water masses) appear to play an important role in the advection and/or retention of fish larvae and other planktonic particles. (Iwatsuki 1989, Nakata 1996, Townsend & Pettigrew 1996). A large number of observations show a coincidence between frontal zones and enhanced

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concentrations of fish larvae (Bolz & Lough 1984, Kiørboe et al. 1988, Campana et al. 1989, Munk & Nielsen 1994, Lochmann et al. 1997), and lately evidence of the specific influence of frontal processes has been given by a number of biophysical modelling studies exploring drift and dispersive processes in well-known nursery areas of fish larvae (e.g. Werner et al. 1993, 1996, Franks & Chen 1996, Manning et al. 1997). These studies demonstrate the importance of small-scale density structures and of the vertical component of the flow field in the vicinity of frontal features. Flow convergence and divergence are particularly intense near fronts, and fish larvae and other plankters can potentially be concentrated while they counterbalance a downward flow in the frontal zone. Franks (1992) used a modelling study to illustrate how patchiness of plankton organisms may arise through zones of retention or accumulation, and how the degree of aggregation is closely connected to the strength of the vertically directed swimming. Consequently the aggregation/retention process might be influenced by a series of factors which direct the horizontal/vertical distribution of the organism. Among these are physical factors such as light, turbulence and water temperature, as well as the biological factors such as larval buoyancy, swimming performance and availability of prey (Sclafani et al. 1993).

When concentrated in the vicinity of a frontal zone, fish larvae might benefit from the accumulation of prey organisms here. The coincidence between elevated densities of fish larvae and their copepod prey has been described for a number of frontal systems (e.g. Munk et al. 1995, Napp et al. 1996, Lochmann et al. 1997), and additionally stomach content analysis of larvae across frontal structures suggests that the feeding conditions are improved in the zone (Iwatsuki et al. 1989, Munk 1995). Intensified turbulence in the frontal region, which could increase prey encounter (MacKenzie et al. 1994), would be another advantage, while a negative impact could be expected from an increased number of potential larval predators in the front. Obviously both physical and biological processes in the frontal region are of great importance to the fish larvae residing here.

Munk et al. (1995) reported on a study where the distribution of cod larvae followed the path of a frontal zone along the shelf break in the northeastern North Sea. This investigation, performed in 1992, was continued in the following years (1993–1994) in order to verify the consistency of the observations, and to gather further information about the variability in frontal formation and larval fish distributions. Fish species other than cod were distributed in the vicinity of the frontal zone, and we included 4 other species of gadoid larvae in our continued investigations. These

species were whiting, saithe, Norway pout and haddock. Beside the 3 main study years, a pilot study was carried out in 1991, and in this paper we will present observations from the 4 consecutive years, 1991 to 1994. Based on the earlier findings, we hypothesise that each larval species has a unique relationship to the frontal hydrography. Consequently, we focus on similarities and differences between distributional patterns of the larvae of the different gadoid species, and on their relative distances to the frontal zone. Further, we look into the interannual variability in biology and physics and consider the potential consequences of frontal variability on nursery area characteristics.

MATERIALS AND METHODS

Hydrography. The area of investigation is illustrated in Fig. 1. Along the northern Danish coast the shelf extends 30 to 60 nautical miles (n miles) offshore, and from the shelf break the bottom slopes abruptly to the deep of the Norwegian Trench (>600 m). In contrast, along the Norwegian coast the shelf is very narrow and the shelf break is here found less than 10 n miles offshore. The surface circulation at the Danish coast is dominated by the fresh Jutland Coastal Current (JCC) flowing in an eastward direction, while the fresh Norwegian Coastal Current (NCC), a continuation of the Baltic outflow (BO), flows in a westward direction along the Norwegian coast. The deepwater circulation is dominated by water of Atlantic origin (AW) which enters the Skagerrak through the deep Norwegian Trench, while intrusion of shelf water from the North Sea (NSSW) is observed off the Danish coast. Rodhe (1996) and Gustafsson & Stigebrandt (1996) provide more detailed information about water masses and currents in the investigation area.

During the study the area was surveyed by up to 3 research vessels for periods of about 2 wk in May. Four surveys were carried out, dating from 15 May 1991, 10 May 1992, 1 May 1993 and 8 May 1994. Sampling during the survey in 1992 was carried out in a 10' (latitude) \times 20' (longitude) grid, while sampling during the other surveys followed cross-bathymetric transects using a station distance of either 5 or 10 n miles. In 1991 the transects only covered the Skagerrak region. Temperature and salinity were profiled using a Neil Brown Mark III CTD, except for a restricted number of stations in the eastern part of the investigation area where the profiling was carried out by water-bottle sampling at 5 or 10 depth intervals. From 1991 to 1993 fluorescence was profiled using a fluorometer mounted on the CTD; these measurements were converted to chlorophyll *a* by the procedure described in Munk et al. (1995). In 1994 chlorophyll *a* profiling was

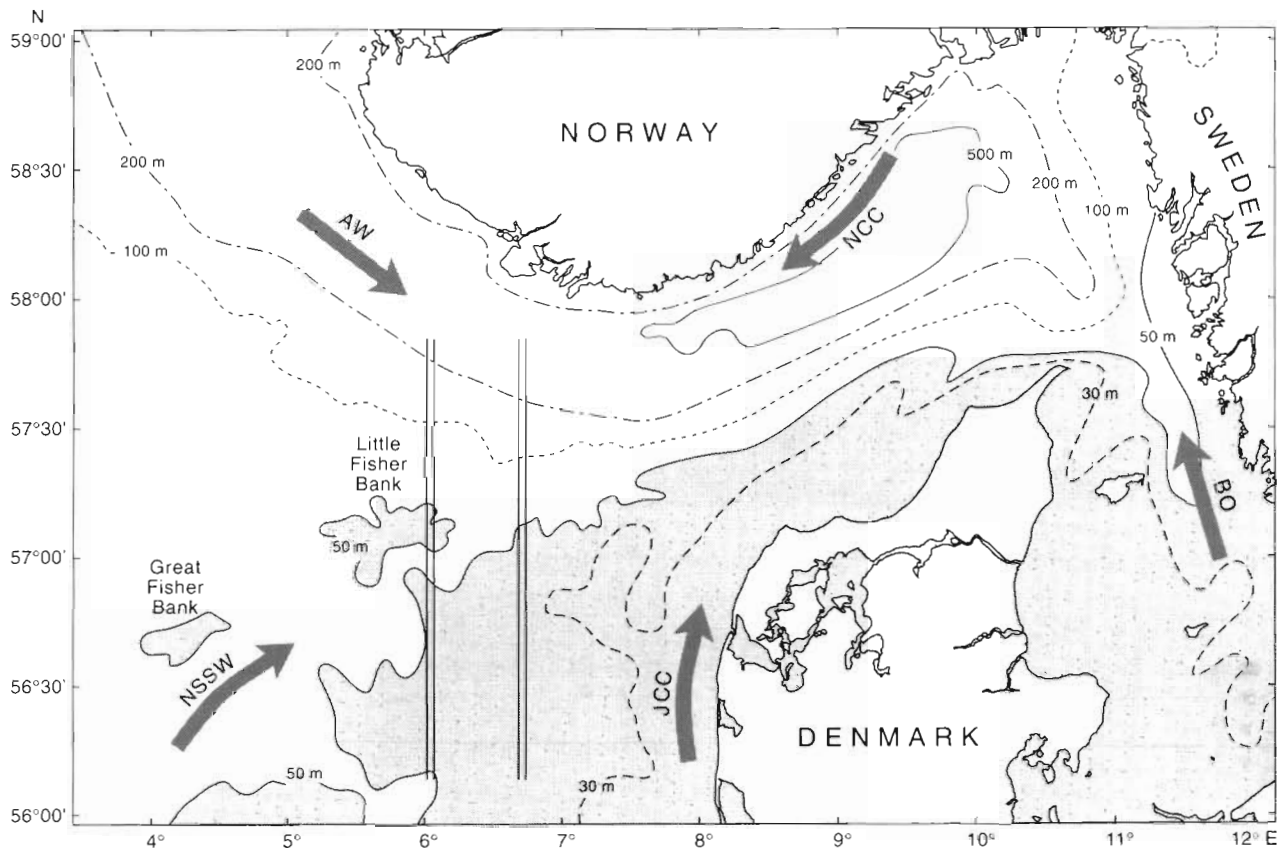


Fig. 1. Area of investigation: the northeastern part of the North Sea, the Skagerrak between Norway and Denmark, and the Kattegat between Denmark and Sweden. Isolines illustrate bottom topography, shading demarcate areas shallower than 50 m. Arrows denote major currents; AW: deep Atlantic inflow, NSSW: North Sea Shelf Water, BO: Baltic outflow, JCC: Jutlandic Coastal Current, and NCC: the Norwegian Coastal Current. Two double lines show the transects at 6°E and 6°40'E

only carried out on a single transect using bottle sampling at 10 m intervals. Larval/juvenile fish were sampled using a ring net of 2 m diameter. The gear has a 2-legged, 10 m long bridle and is equipped with a 13 m long black net of 1.6 mm pore size (see Munk 1993). At each station the gear was towed in an oblique haul to 5 m above the bottom. The wire was deployed and retrieved at speeds of 25 and 15 m min⁻¹ respectively, while ship speed was kept at 1.5 m s⁻¹. A flowmeter mounted in the centre of the net opening was used for estimation of filtered water volume; the volume was in the order of 6000 m³, dependent on the water depth. All fish were immediately preserved in 96% ethanol and later identified to species and measured in 1 mm intervals for length. Abundance of fish larvae per unit area was estimated using information on sample size, filtered water volume and water depth.

Along every cross-frontal transect the station with maximal density of a given fish species and the station with maximal water density at the surface were identified. The distance between these 2 stations was estimated within the 10 n mile resolution of sampling and expressed either as an inshore (–) or offshore (+) dis-

placement of larval density peaks. Frequency diagrams of the estimates for all transects were produced for all available species-year combinations.

Isopleths of data were produced in the programme Surfer®, using an interpolation between datapoints based on the square of the inverse distance. Larval abundance within the area of investigation was found from an interpolated grid of larval density using the function 'Volume' in the programme. The method is described in Press et al. (1986).

RESULTS

Hydrography

The hydrography at the shelf slope was characterised by a doming of water of higher density. We use the measurements along 2 specific transects to illustrate the observed density structure at the shelf slope off the Danish coast. These transects cross the shelf break along 6°E and 6°40'E (illustrated by double lines in Fig. 1); both were visited during the surveys in

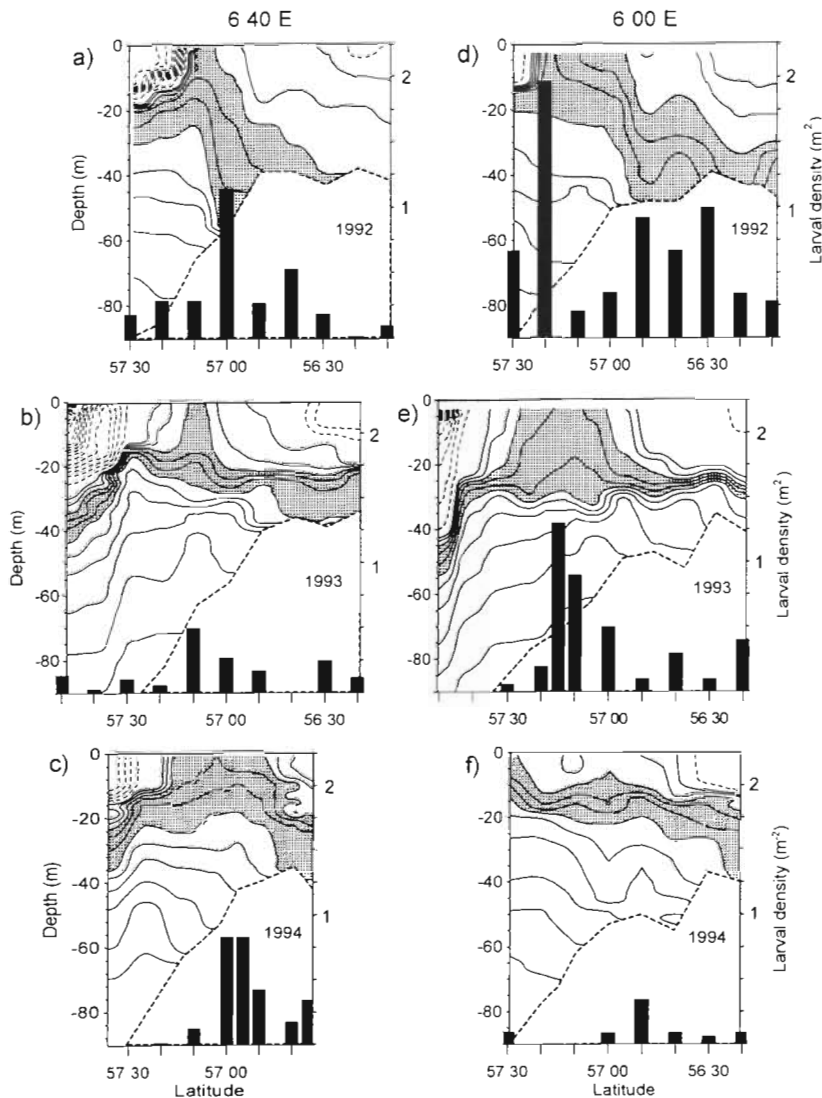


Fig. 2. Variation in water density and abundance of cod larvae along 2 transects during 3 of the years of investigation. (a–c) Variation along 6°40' E; (d–f) variation along 6°E. Transect length differs between years, graphs are aligned according to latitude. Values on left axis denote water depth in meters; values on right axis denote larval density in no. m⁻². Bars along transects show variation in larval density. Solid isolines show water density for each 0.1 kg m⁻³; dashed lines illustrate intervals of 0.3 kg m⁻³. The interval between 1027.2 and 1027.5 kg m⁻³ is shaded

1992, 1993 and 1994. Fig. 2 shows the vertical profiles of water, the isopycnals are drawn in intervals of 0.1 kg m⁻³ and a specific interval (1027.25 to 1027.45 kg m⁻³) is shaded in order to elucidate differences between profiles. A characteristic of all transect profiles was the doming of the pycnolines. At 6°40' E in 1992 (Fig. 2a) the inclination of isolines was very distinct, while in 1993 (Fig. 2b) a marked thermocline interrupted the inclination, and no isolines could be followed from surface to bottom. In 1994 (Fig. 2c) the inclination of pycnolines was again not as prominent as in 1992 and this

year the dome was situated further in-shore. The influence of the shallow banks on the shelf was evident in 1992 with inclined isopycnals around the bank (Fig. 2d), while this pattern was less prominent the following 2 years (Fig. 2e,f). The doming was skewed towards the shelf slope; doming of isopycnals occurred further offshore with increasing water depth and water mass density.

The vertical profiles shown in Fig. 2 represent the general trends in density structure of the water column observed during the surveys. The transect along 6°40' E characterises the hydrography observed east of this longitude, which is influenced by the steep shelf slope in the Skagerrak area. The transect along 6°E represents the hydrography in the westernmost part of the investigation area, where the slope is less steep and the shelf break includes shallow banks.

The density structure of the water column, presented in Fig. 2, illustrates the formation of 1 or more frontal zones, identified by the steeply inclining isopycnals that separate the shelf water from the denser water mass of Atlantic origin. An increase in water mass density in the upper layers was seen as the surface manifestation of the boundary zone between the water masses. We considered the frontal zone(s) off the Danish coast to be located at the position (station) where water density reached the highest value along cross-frontal transects (at 20 m depth). The location of the zone identified by this measure was expected to parallel the results of other possible measures of frontal position, e.g. the site of maximum vertical gradient in isopycnals. Along most of the cross-shelf transects 1 maximum in surface water density was found; however, in the vicinity of the banks a second local maximum was frequently registered.

The positions of the front obtained by the analysis are illustrated in Fig. 3. Symbols indicate positions where a cross-shelf maximum in water density was observed (at 20 m). Note that in the western part of the area 2 maxima could be found in the cross-shelf direction. The sampling in 1991 did not include the area west of 7°30' E. Each year the front followed an isobathymetric course; however, the relative position of the front differed among the years of investigation.

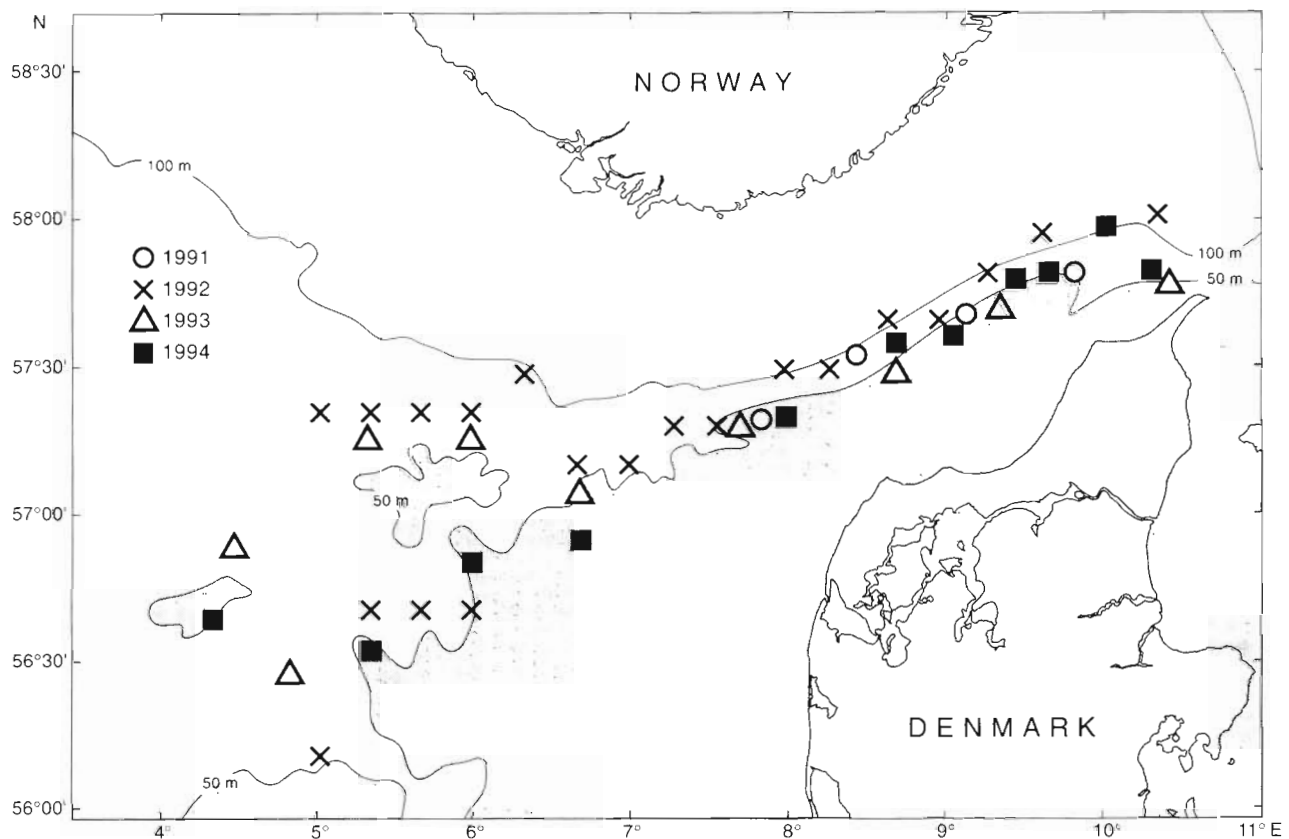


Fig. 3. Demarcation of frontal positions identified by surface maxima in density. Different symbols indicate observations from the different years

The observations illustrate a marked interannual difference in water depth at frontal position; the shallowest position of the front was observed during the survey in 1994.

The inclination of isopycnals was predominantly due to salinity differences, but an upwelling of colder water, seen as a local minimum in surface temperature, was often found displaced from the maximum in surface salinity. The distance between the 2 domes differed over the area and between the years of investigation. Fig. 4 illustrates the horizontal distance between temperature minima and salinity maxima at either 2 m depth or 20 m depth, registered within the 5 or 10 n mile resolution of our transect sampling. The observations in 1992 and 1994 showed a marked variation in the relative position of the temperature minimum, from an inshore displacement of about 20 n miles in the North Sea area to an offshore displacement of about 10 n miles at the easternmost observations in the Skagerrak. In 1991 and 1993 the temperature minimum often coincided with the salinity maximum; observed displacements of temperature minima were solely offshore in 1993 and solely inshore in 1991.

Munk et al. (1995) describe an enhancement of phytoplankton concentration in the vicinity of the

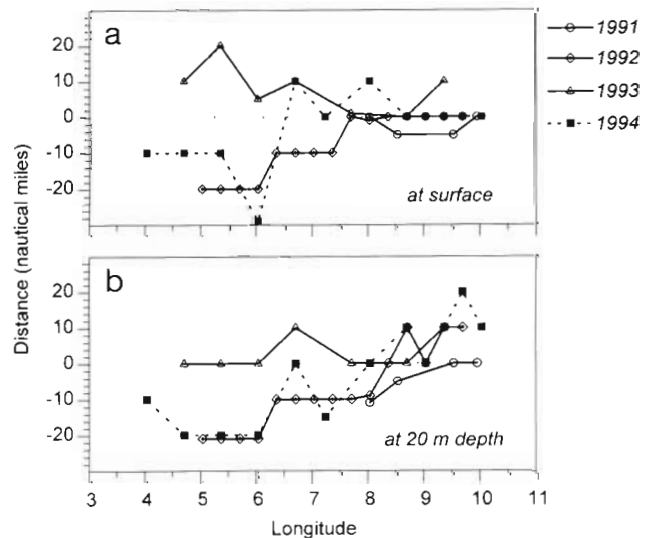


Fig. 4. Distance between the positions of temperature and salinity fronts, identified by minima in surface temperature or maxima in surface salinity, respectively. Measurements either at (a) 2 m depth, or (b) 20 m depth. Distances between fronts are in n miles within the 10 n mile (occasionally 5 n mile) resolution of transect sampling. Negative distance denotes observations when the temperature front was inshore of the salinity front (relative to the Danish coast), positive distance when it was offshore

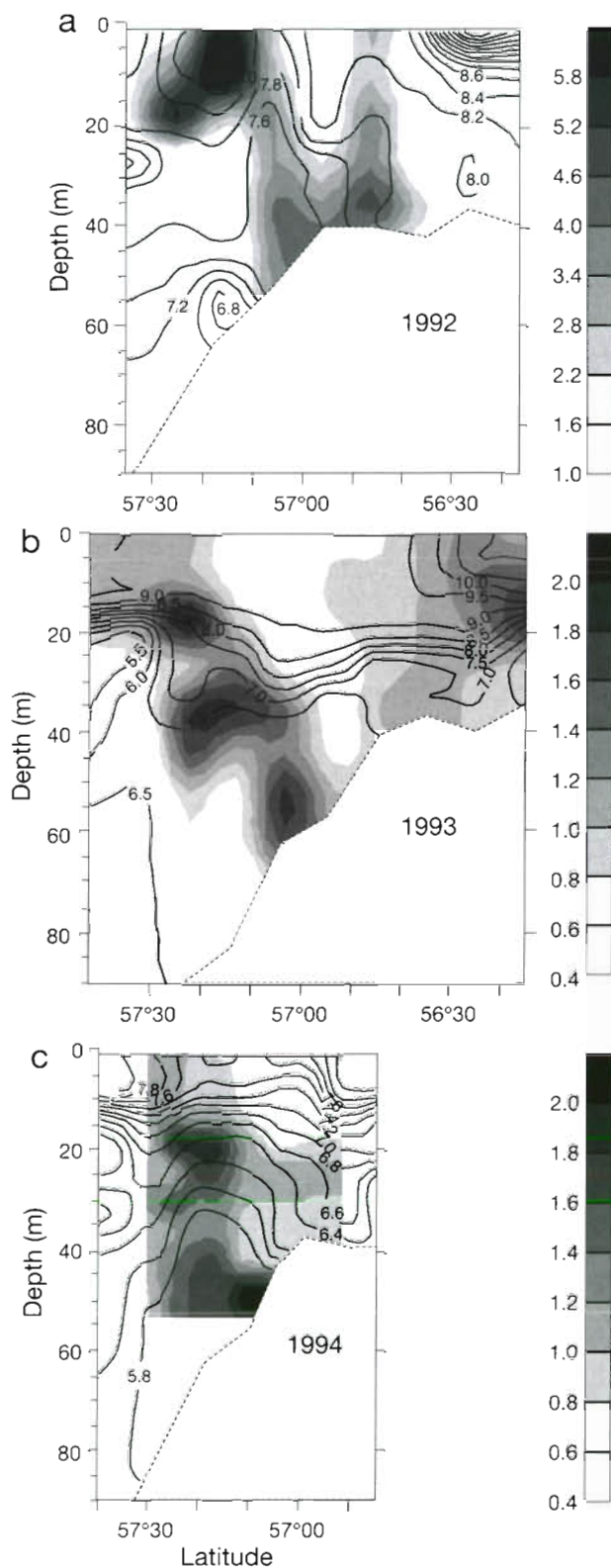


Fig. 5. Variation in temperature and chlorophyll a concentration at the transect along 6°40' N. (a–c) Years 1992 to 1994. Isotherms are shown using intervals of 0.2°C; chlorophyll concentration is shown by shading, increasing by (a) 0.6 mg m⁻³ or (b,c) 0.2 mg m⁻³

frontal zone based on the findings from 1992. This linkage was verified by the observations made during the other surveys. Moreover, a comparison between the respective profiles of temperature, salinity and chlorophyll throughout the years of investigation, indicates that the phytoplankton enhancement (i.e. the maximal chlorophyll a concentration integrated for the water column) was more closely linked to the doming of colder water than to the salinity profile. Fig. 5 illustrates yearly observations along 6°40' N of elevated chlorophyll a concentrations in the areas of doming isotherms.

Fish larvae

The description of larval fish distribution is based on a total of 474 hauls performed during the study. A number of different fish larval species were observed in the area, of which the gadoid species and a number of flatfish species dominated. Only the gadoid species will be dealt with here, these being: cod *Gadus morhua*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus*, Norway pout *Trisopterus esmarki* and saithe *Pollachius pollachius*. In Table 1 the mean lengths and the estimated abundances of larvae are given. Abundance estimates are only made for the area specified in the legend of Table 1, with no estimates made for 1991 due to the limited coverage. The cross-frontal distribution of cod larvae on 2 of the transects is illustrated by inserted bars in Fig. 2, while the observed distribution patterns of all gadoid larvae along all sampling transects are shown in Fig. 6. This figure also illustrates the transect positioning during each of the years. Due to preservation problems at some of the stations in 1991, this year's quantitative

Table 1. Abundances of gadoid larvae within the area bordered by coastlines and 56°N, 58°45'N, 4°E and 11°30'E. Estimation procedure as described in text. Mean length of gadoid larvae measured as standard length of preserved specimens. –: no estimation

Year	Cod	Whiting	Haddock	Norway pout	Saithe
Abundance (no. × 10¹⁰)					
1991	–	–	–	–	–
1992	2.59	1.59	1.13	6.38	0.15
1993	2.39	0.22	0.35	1.94	0.03
1994	0.96	0.38	0	0	0.01
Mean length (mm)					
1991	17.4	12.4	12.4	15.9	20.2
1992	20.1	16.4	15.6	15.4	19.6
1993	20.1	17.8	16.8	17.2	25.6
1994	17.6	17.8	–	–	–

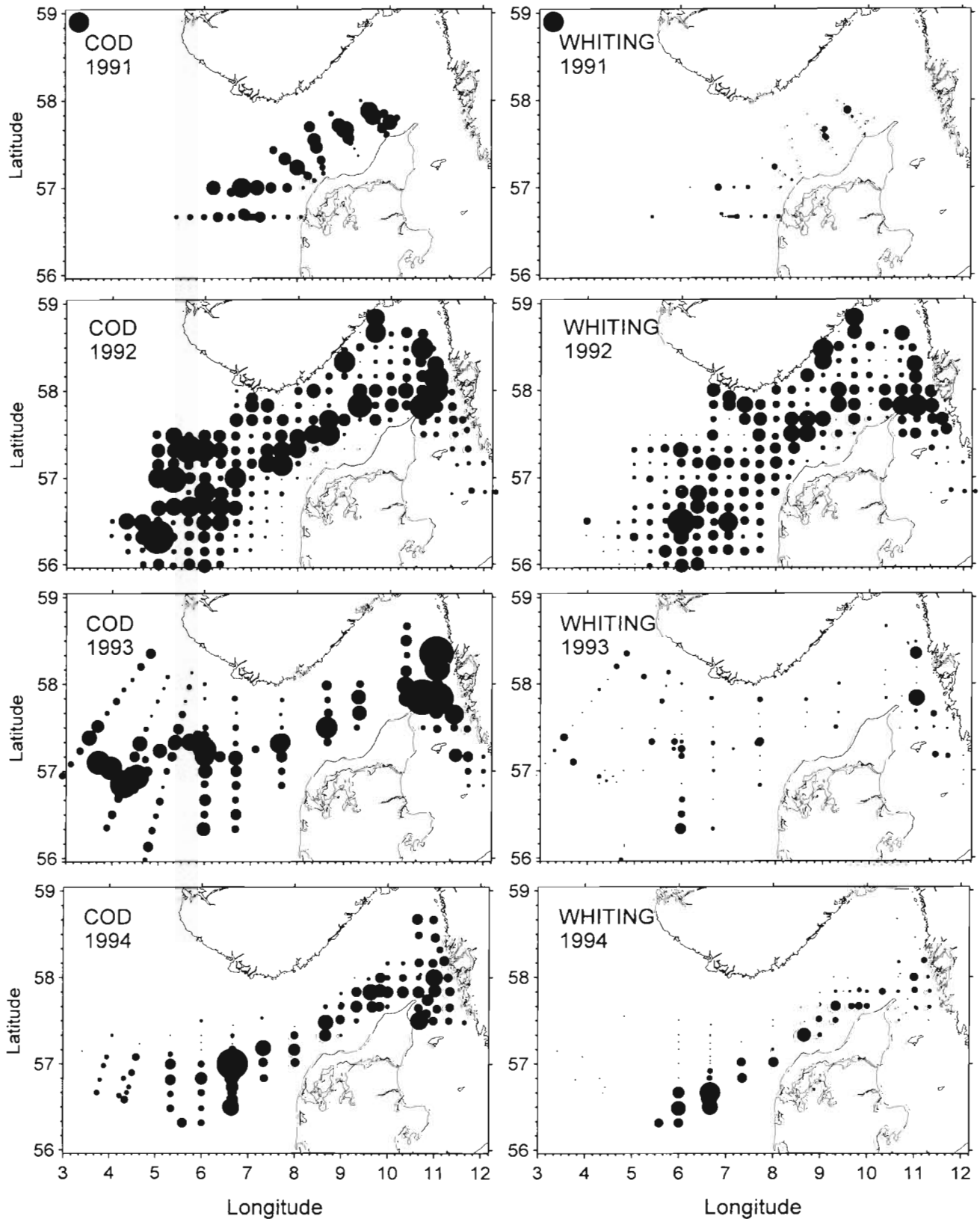


Fig. 6. Distribution of cod *Gadus morhua* and whiting *Merlangus merlangus*, and (overleaf) haddock *Melanogrammus aeglefinus*, Norway pout *Trisopterus esmarki* and saithe *Pollachius pollachius* during the 4 years of investigation. Area of filled circles illustrates densities in no. m⁻²; filled circle inserted in the upper corner of each panel for 1991 illustrates a density of 1 m⁻². Smallest circles denote sampling positions where no catch was recovered

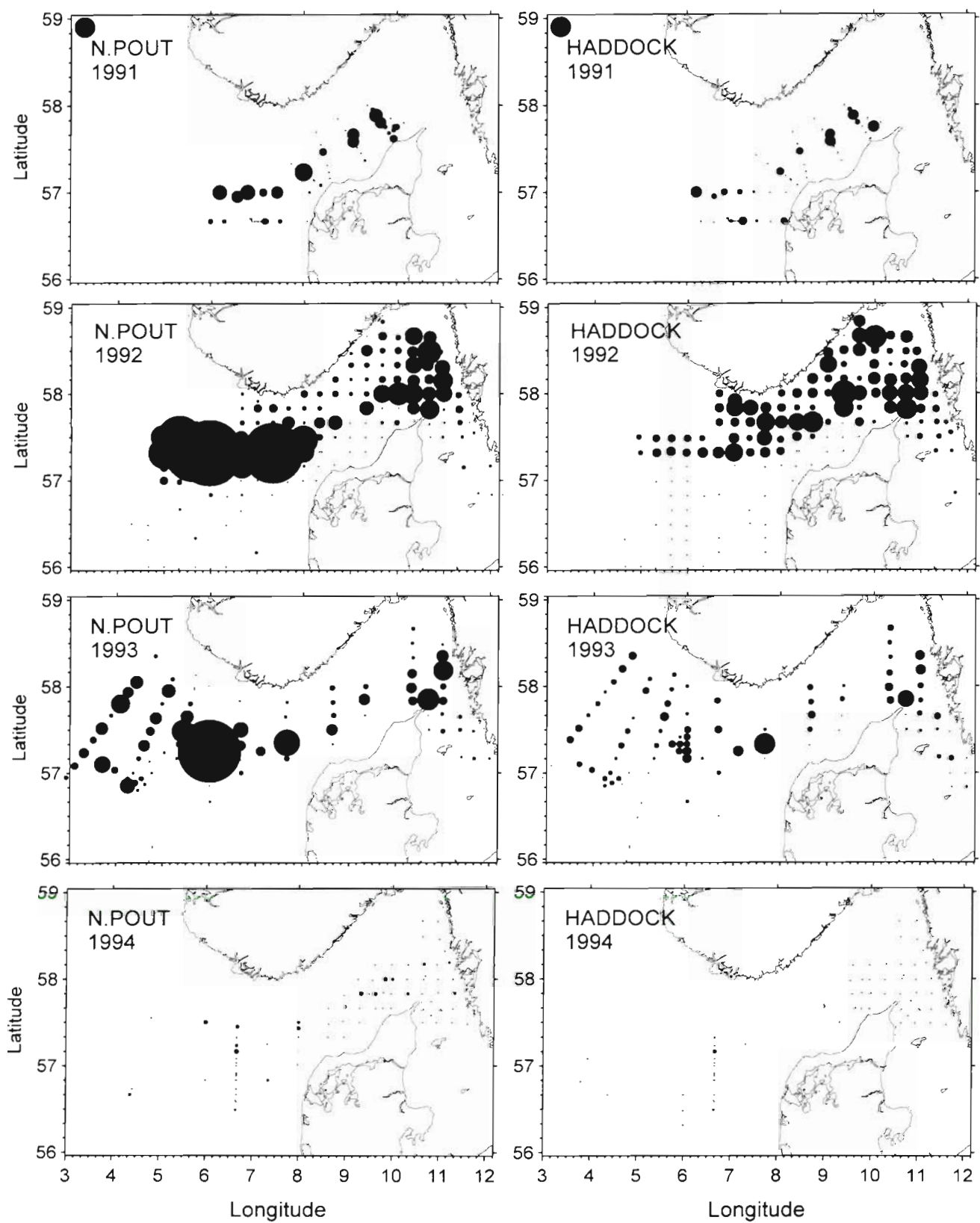


Fig. 6 (continued)

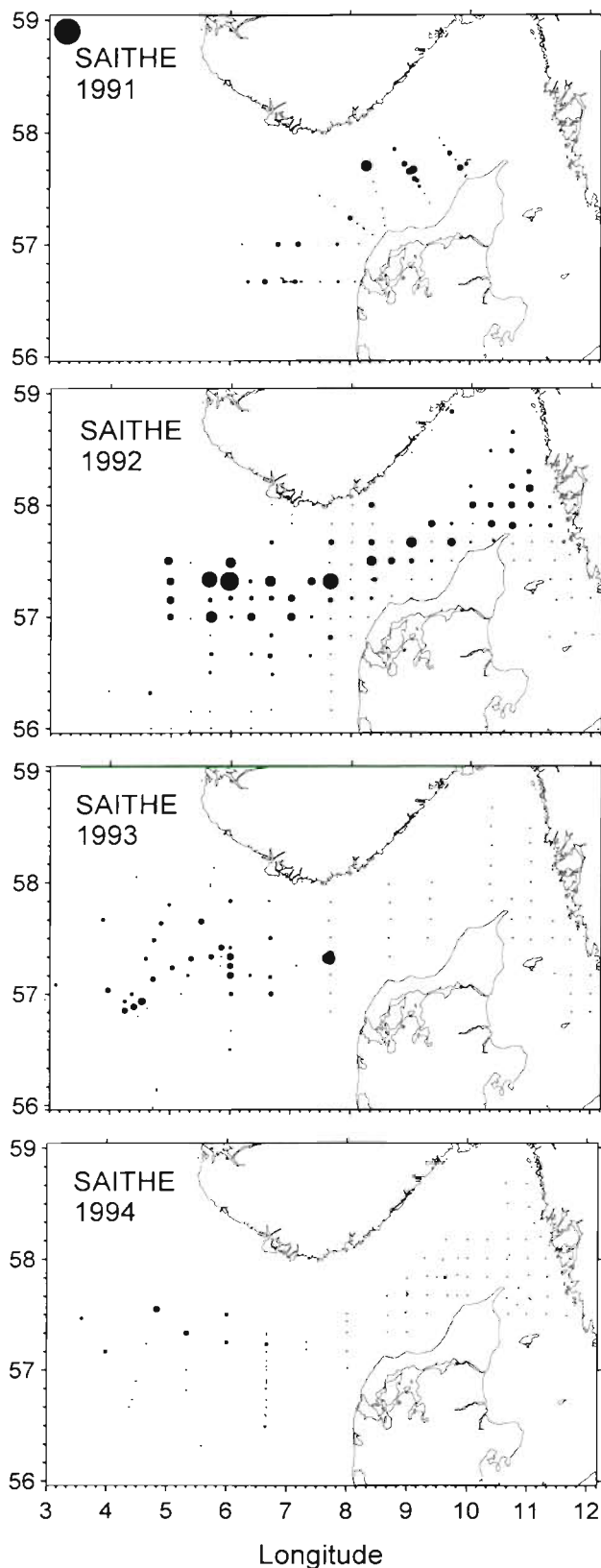


Fig. 6 (continued)

information for haddock, Norway pout, and whiting is limited.

During the period of investigation, cod and Norway pout were the most abundant larval fish species; however, the high total abundance of Norway pout resulted from a limited number of very high estimates (up to 23 m^{-2}), while cod was more widespread across the area. The abundances of all gadoid larval species tended to peak within restricted zones following an isobathymetric course. The concentrations of larvae were observed at the shelf slope off the Danish coast and, to a smaller extent, close to the Norwegian coast. Visual comparison between the distribution of larvae and the frontal zone (as depicted in Fig. 3) revealed examples of correspondence between the along-shelf path of larval concentrations and the front. The association was analysed by a comparison of cross frontal distances between the peak densities of larvae and the frontal positions shown in Fig. 3. The graphs in Fig. 7 show the distances observed for each species and year. Peak densities are not distributed randomly along transects while a high degree of coherence between peaks in larval abundance and the frontal zone is seen (zero distance, hatched bars). A *t*-test shows that in 10 out of 14 species-year combinations the mean distance between peaks and front was insignificantly different from zero ($p > 0.05$ in these cases). However, in some of the species the peak abundance tended to be displaced either inshore or offshore of the front, indicating a species-specific association between hydrography and larval distribution. For example, whiting was in general distributed to the inshore side of the front, while Norway pout and haddock were distributed offshore the front. Cod and saithe were either found solely in the front (1993) or slightly inshore of the front.

Differences between species and years of sampling were examined by an analysis of variance in the programme GLM (SAS Institute Inc., Cary, NC). The difference between species in their distances to the front is highly significant ($df = 4$, $F = 16.2$, $p < 0.001$), while the effect of year is insignificant ($df = 9$, $F = 1.5$, $p > 0.14$). A pairwise *t*-test of differences among species (in the GLM programme) revealed significant differences between pairs ($df = 136$, $\alpha = 0.05$, $MSE = 53.3$) except in 2 combinations, i.e. saithe and cod were not different and Norway pout and haddock were not different.

DISCUSSION

The present series of hydrographical observations at the shelf slope of the North Sea and the Skagerrak shows that the frontal activity observed here in May 1992 (Munk et al. 1995) is a recurrent phenomenon.

Other investigations have made similar observations; for example, Gustafsson & Stigebrandt (1996), in an analysis of time-series data, found particularly distinctive frontal zone formation in the Skagerrak area during May. The observed front at the shelf slope off the Danish coast is of the retrograde type and is conceived as the inclined region that separates North Sea shelf water from Atlantic water intruding into the Norwegian Trench. Willmott & Collings (1997) modeled the

maintenance of shelf break fronts and illustrated the possible variability in frontal position and shape in relation to water mass properties and depth. We observed marked interannual and along-shelf variability in the frontal characteristics; some of this might stem from changing water mass properties as described by Willmott & Collings (1997), and some might be the result of wind events and/or changes in the coastal currents. The composite frontal structure in the

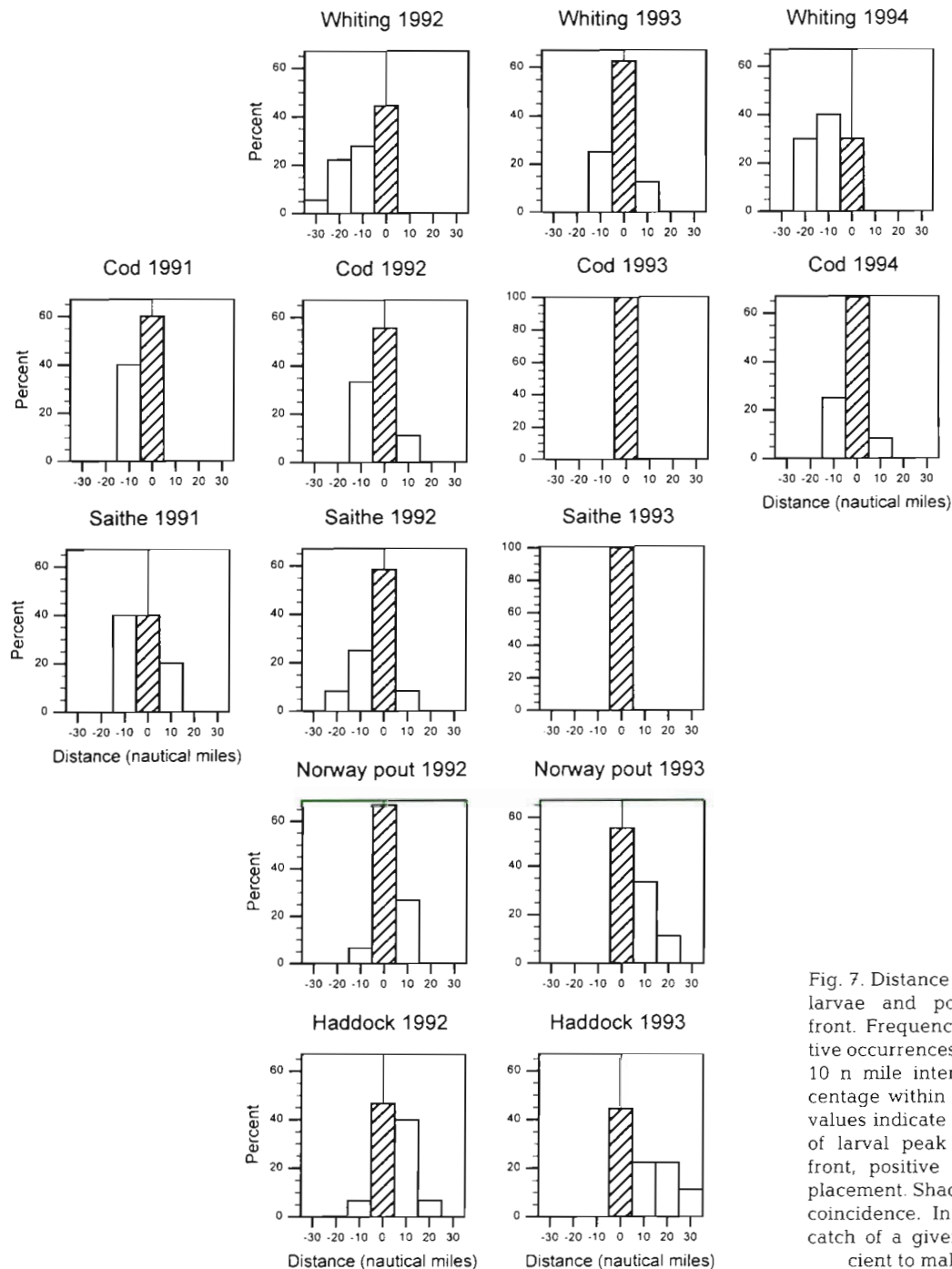


Fig. 7. Distance between peak density of larvae and position of hydrographic front. Frequency graphs show the relative occurrences of distance categories of 10 n mile intervals, expressed as percentage within each category. Negative values indicate an inshore displacement of larval peak density relative to the front, positive values an offshore displacement. Shaded bars show immediate coincidence. In some of the years the catch of a given species was not sufficient to make reliable estimates

southwestern part of our investigation area in the area of the Fisher Banks could be interpreted as a separation into 2 fronts, a shelfbreak front and a tidally mixing front. The frontal structure in a comparable area, the Georges Bank region in the Mid Atlantic Bight, has been interpreted to be 2 such parallel fronts (Churchill & Manning 1997).

Our findings of coexisting gadoid larvae at the shelf slope of the North Sea are in accordance with historical observations of adult and juvenile distributions of these fish. Observations were made in the period 1974 'International 0-group Gadoid Surveys' (Holden 1981, Anonymous 1984), when juvenile gadoids were surveyed in an area covering the shelf slope from the Skagerrak to the Orkney/Shetland Islands. The surveys covered the period from mid June to mid July, and the gadoids in the small-meshed trawl were of lengths 5 to 7 cm. During these surveys, gadoid abundance peaked in the area of the shelf slope, and a comparison of the gadoid spatial distributions reveals a cross-shelf difference resembling the structure observed during the present study on the larvae. Juvenile whiting was predominantly positioned in the more shallow areas, haddock and Norway pout in the deepest areas and cod and saithe were found in between.

The present series of observations on larvae in the area of the shelf slope supports the hypothesis that larval nursery areas are linked to frontal features. The linkage was evidenced by the repeated observations of parallel along-shelf locations of fronts and larval distributions. The distributions of gadoid larvae overlapped to some extent, but distributions of 3 groups of the gadoid larvae were significantly different from each other. A structuring of larval communities in the cross-bathymetric direction is frequently observed (Cowen et al. 1993, Richards et al. 1993) and possibly founded in different spawning strategies by the fish species. It appears, however, that frontal dynamics plays an important role in the maintenance of spatial separation and interrelations between larval species (see also Fortier et al. 1992, Sabates & Olivar 1996). While the hydrographic front might serve to aggregate/accumulate planktonic organisms, the frontal circulation pattern and limited cross-frontal flow result in a wide range of physical regimes, and maintain a number of different biological assemblages within the frontal region.

The present investigation covers the same season during 4 consecutive years, and, while fundamental observations such as the establishment of hydrographic fronts and the connection between these and larval distributions were repeated, we also found interannual differences of potentially great importance. Because of the dynamic character of the frontal hydrography, any comparison between yearly observations

hinges on the assumption that the picture depicted from 1 annual survey emphasises conditions that prevailed long enough to significantly influence larval life. A study on the persistency of our transect-based observations of hydrography and biology in 1994 illustrates this (Munk 1995). During the survey in 1994, we made repeated measurements along the same cross-frontal transect for a period of 6 d and found that during this period the observations (of frontal characteristics and larval distributions) could be replicated with less than 5 n miles variation along the transect. Further support is found from the investigations in 1992, when the May cruise was followed by another cruise 2 wk later which verified the observations of larval concentrations in the vicinity of the frontal zone in the western part of the area (see Nielsen & Munk 1998). These findings indicate that each of our surveys illustrates prevailing conditions during a period of at least a week.

Apparently, major interannual differences in frontal hydrography, as observed during our yearly May surveys, were paralleled by differences in larval distribution patterns. The outstanding strength and prevalence of the front(s) in 1992 was reflected in an outstandingly high abundance of all gadoid larvae; this year, whiting and cod were distributed both in the frontal area at the shelf slope and in the frontal zone around the banks. In May 1993 the water column was dominated by a strong thermocline and both frontal processes and larval abundances were less prominent. Whiting and cod larvae were this year mainly distributed in the frontal area at the shelf slope. Finally, in 1994, when the extension of the front was limited in the area of study, the distributions of whiting and cod larvae were restricted and Norway pout, haddock and saithe virtually disappeared from the investigation area.

This striking decline in larval Norway pout and haddock abundance in the area in 1994 might stem from changed spawning by the adult stock. However, another possibility is advective losses (vagrancy) of larvae from the populations due to a weakening of the retentive capacity of the frontal processes in 1994. The potential importance of seaward losses of larvae to less favourable areas is discussed by Sinclair (1988) and Fortier & Gagne (1990), and according to the member/vagrant hypothesis proposed by Sinclair (1988) larval recruitment would depend on the integrity of the hydrographical structures that limit the dispersion of the early stages. The effect would relate both to the maintenance of the unity of the population during the larval stages (which would lead to imprinting and homing behaviour) and to the prevention of larval vagrancy.

Our observations of distributional differences among the gadoid larvae suggest that the risk of seaward loss

of larvae would differ among species. The larval Norway pout and haddock, which previously were observed on the offshore side of the frontal zone, might have been more severely influenced by a coastward movement of the frontal zone in 1994 than the other species. The disappearance of these species, along with a restriction and shoreward movement of larval distributions of cod and whiting, signifies that variations in frontal zone formation have a diverse influence on the integrity of the larval populations. Hence, while different larval assemblages are resident in the frontal region and share a variety of environmental conditions, their responses to frontal variability in terms of dispersal, growth and survival might differ considerably.

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